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The Coastal Movements of Returning Atlantic Salmon, *Salmo salar* (L.)

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The Coastal Movements of Returning Atlantic Salmon, *Salmo salar L.*

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Introduction

The Atlantic salmon makes extensive migrations during its life history. After an initial phase of fresh water development the salmon descend their river of origin and enter the sea, where they may later be caught a considerable distance away. One or more years later the well grown and sexually maturing fish reappear at the coast and re-enter fresh water, where spawning takes place. The fish may later go back to the sea, perhaps returning to fresh water once more to spawn a second time. Of the fish which are caught on return, the majority are recaptured either on the coast close by or in their natal rivers despite their prolonged and distant sojourn in the sea.

This paper describes preliminary observations on the movements of salmon on their return to coastal waters off the east of Scotland. Fish caught at a coastal netting station were tagged with acoustic transmitters, released into the sea and their subsequent movements followed by means of a hydrophone receiver fitted to a small boat. Several fish were followed into a river, and their movements into the estuary are described. In addition, the behaviour of fish in the vicinity of coastal netting stations is reported.

Methods

The study area

The fish were captured in bag nets fished by Messrs Jos. Johnston & Sons Ltd at their Rockhall station. The station is 8 km north of Montrose on the east coast of Scotland and lies at the head of a small southward facing bay. (Fig. 1). The station itself is backed by rocky cliffs, but is separated from the River North Esk, 3 km to the south, and from Montrose by a series of extensive, gently sloping, sandy beaches. To the north, along rocky shores, are the small harbours of Johnshaven and Gourdon, the latter immediately south of the mouth of the River Bervie.

Fish caught at the Rockhall station, tagged conventionally and released by one of us (WMS) – have subsequently been recovered from several Scottish rivers, including the Dee, Don, Deveron, Spey, Findhorn and Nairn to the north, and the Tay and Tweed to the south. Many of the Rockhall fish are recaptured in the rivers North and South Esk, though a significant proportion move northwards. (In 1950 and 1951 nearly half the fish recaptured had migrated northwards.)

At the time this study was made 12 bag nets were fishing at Rockhall, in four lines running out from the shore (two, one, six and three bag nets per line). Each net consisted of a leader stretching seaward to meet a bag or trap, with the opening of the bag facing towards the shore (Fig. 5).

South of the Rockhall station a series of bag and stake nets (Fig. 1) stretched from the shore on either side of the mouth of the North Esk.

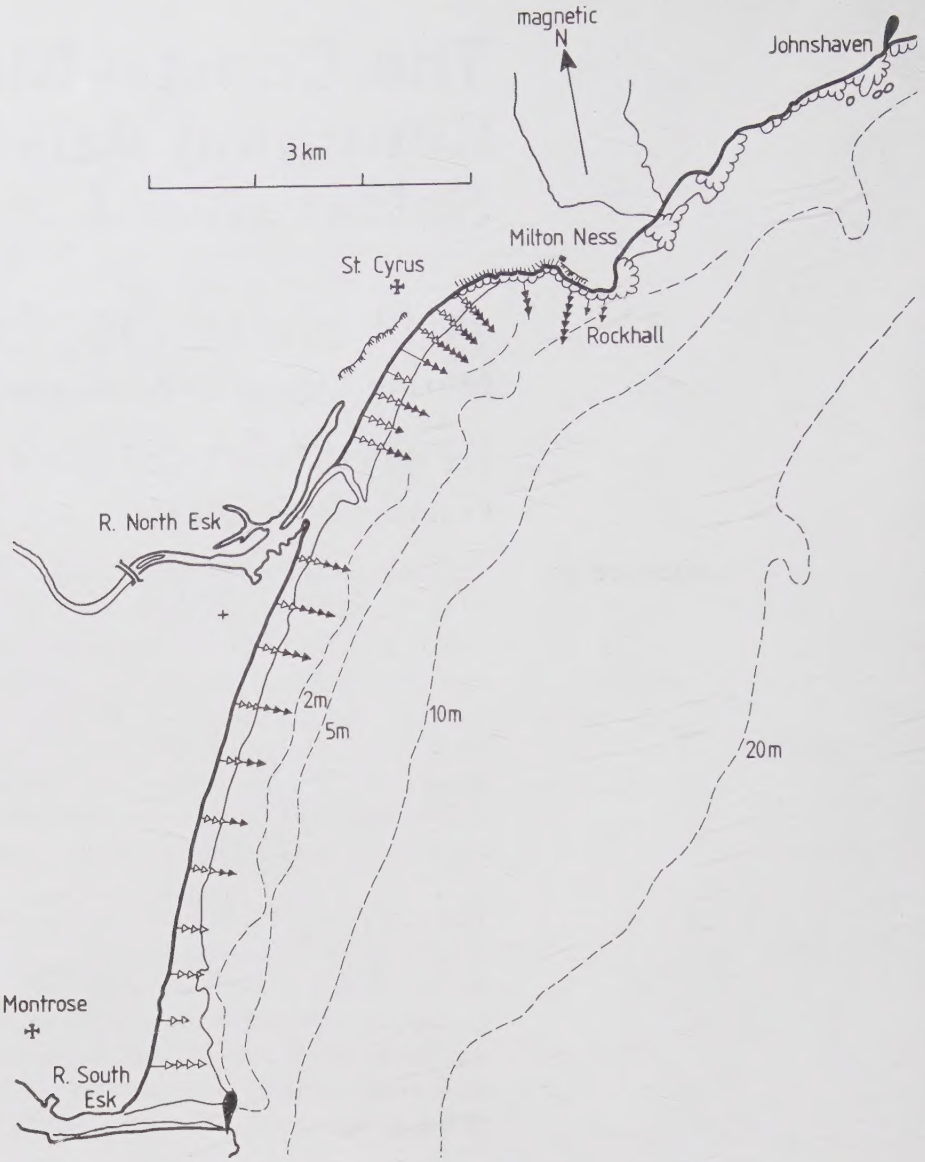

Figure 1. Montrose Bay, showing the Rivers North and South Esk and the fishing stations of Rossie, Charleton, Watermouth, Kirkside, Woodston and Rockhall. Fly nets are shown as white triangles, and bag nets as black triangles.

Technique of capture and tagging

The experimental fish were taken from a bag net on the second fishing of the day, some 6 hours after a previous fishing. After careful removal by hand each fish was immediately transferred to a black polythene bag containing an anaesthetic solution in seawater (1 part in 10,000 MS 222). When the fish was deeply sedated, but before respiratory movements had ceased, it was transferred to a wooden measuring board, measured, a sample of scales removed and a conventional hydrostatic tag inserted just in front of the dorsal fin. A previously prepared acoustic transmitter was then inserted into the mouth and gently pushed into the stomach.

The fish was subsequently revived in fresh seawater, placed in a weighted cage covered with fine mesh cotton netting (1 m x 1 m x 1.5 m) and sunk to the sea bed, with its position marked by a small float. After 12 hours to allow the fish to recover from handling the cage door was opened from the surface by passing a messenger weight down the float line to trigger a catch. The fish was allowed to swim from the cage, and then followed by two boats provided with tracking equipment.

Tracking equipment

The acoustic transmitters, supplied by the Lowestoft Fisheries Laboratory, produced 1.5 ms long pulses of sound every 1.5 s at a frequency of 75 kHz. The devices were cylinders 14.7 mm in diameter, and 58 mm long, with an external coating of hard epoxy resin. At one end a small cap of dental wax covered the switch terminals.

The transmitters were tracked by means of two directional Lawson tunable hydrophone systems, each mounted beneath a small boat. Each hydrophone consisted of a ring-shaped transducer mounted within a reflective plastic cone giving a beam width of 40° (measured at the 3dB down points). The device was fixed to the end of a plastic rod projecting beneath the keel of the boat. One vessel was an inflatable propelled by a 25 hp outboard motor, and the other a launch propelled by a 75 hp diesel engine. The hydrophones were rotated to yield the bearing of the fish from each vessel. The position of the vessels with respect to the shore was determined either by means of prismatic compass bearings on prominent landmarks, or by means of sextant readings on objects of known height above sea level or on objects of a known distance apart. At night the landmarks were lights at Montrose, Gourdon, Johnshaven and Tod Head.

After release the fish was followed, usually by both vessels maintaining themselves 100 – 200 m away, until it entered a river, when it was followed by the inflatable boat, or simply located from the river bank with a portable hand-held receiver.

Tidal speed and direction during the exercise were determined from Admiralty tables. Water temperatures and salinites were monitored directly by means of a T–S bridge (Electronic Instruments Ltd, type MC5). The water level in the North Esk was measured daily, and the flow estimated.

Results

Six grilse (fish which had spent only one winter in the sea) were tagged and followed. Of these three entered the river North Esk. Details of the six fish and their movements are given in Table I.

Table I

Details of fish released and tracked

Fish	Released	Observations
1. Solon 59 cm grilse age 2.1+ years	4.7.78 12.12 BST	Moved SW towards river North Esk, with flood tide at 7.2 km/h. Signal lost at river mouth at 12.35 and fish presumed to enter river. Fish encountered in trap above tidal reach on 6.7.78.
2. Storm 59 cm grilse age 2.1+ years	6.7.78 13.10 BST	Moved SSW and then S with flood tide at 2.64 km/h. Slowed to 0.75 km/h at high slack water. With onset of ebb tide fish moved E and further offshore at 2.36 km/h. Tracking abandoned under adverse conditions at 19.30.
3. Sigma 61 cm grilse age 2.1+ years	11.7.78 11.05 BST	Moved NE, through 2 bag nets, travelling with ebb tide at 2.74 km/h. Slowed later, swinging E and offshore. At low slack water moved S increasing speed on flood tide to 2.66 km/h. Tracking abandoned under adverse conditions at 18.30.

Fish	Released	Observation
4. Sabrina 61 cm grilse age 2.1+ years	13.7.78 11.02 BST	Moved NE, through bag nets, travelling with ebb tide at 3.00 km/h. Then reversed and moved SW against ebb tide at 1.84 km/h renegotiating many bag nets and stake nets to pass mouth of North Esk. Continued S through stake nets, slowing to 0,59 km/h at low slack water. Reversed course to NNE against flood tide, moving at 1.85 km/h, passing nets and river mouth. After passing through further nets on N side of river reversed course and following flood tide passed again through nets to enter the river mouth at high water. Contact re-established in North Esk and fish followed towards Nab pool. Position in Nab pool confirmed at 14.30 on 14.7.78. Not encountered there on following day.
5. Sugar 68 cm grilse age 2.1+ years	15.7.78 13.14 BST	Wandered in vicinity of Rockhall nets for an hour, then moved E with ebb tide at 1.76 km/h, subsequently slowed, reversing course, and heading rapidly against the weakening ebb tide towards the North Esk at 2.74 km/h. Fish continued S through low slack water, passing around the end of two stake nets, almost reaching the river mouth but then reversing course and moving NE against flooding tide. The fish then reversed again and moved offshore, later returning inshore and passing N and then to S of river. Returned to N side of river against continuing flood tide, entering river mouth at 01.50 on 16.7.78 when tide was ebbing. Subsequently located in Nab pool at 18.10 hours on same day. During inshore movements to N and S of river, fish repeatedly passed through stake and bag nets.
6. Solomon 64 cm grilse age 2.1+ years	18.7.78 09.54 BST	Moved S on flood tide, turning N at high water and proceeding NE, moving faster as tide ebbed, reaching a maximum of 3.3 km/h. At slack water fish slowed, spending a period off the mouth of the river Bervie. On flood tide fish moved SW at 2.5 km/h, later slowing and moving inshore at high water. With new ebb tide the fish returned N along shore at 2.1 km/h, stopping in a bay immediately S of Gourdon harbour at 06.45 hours on 19.7.78. The fish was still in this approximate position at 10.10 on 20.7.78 20.7.78, but could not be found on 21.7.78.

Movements of fish in the sea

It was clear that the behaviour of fish at some distance from a river mouth was strongly related to the flow of the tide. The fish generally moved with the tide, and when the direction of tidal flow changed the direction of movement of the fish altered. The fish may not have been transported

passively since their mean speed often exceeded the tidal flow given in Admiralty tables. Thus, the fish 'Storm' moved in a southerly direction at a speed of 2.6 km/h with the flood tide (the tide predicted as running at up to 2.2 km/h), the fish slowing down at high water and then moving offshore and easterly on the ebb tide at 2.7 km/h (predicted tidal speed up to 1.9 km/h), slowed and moved easterly at slack water, and then moved rapidly to the south on the flood tide (Fig. 2c), increasing speed to about 2.7 km/h (predicted tidal speed up to 1.9 km/h). Similarly, 'Solomon' moved south with the flood tide, turned north with the ebb at a speed of up to 3.7 km/h (predicted tidal speed up to 2.1 km/h), and then slowed at slack water to move south with the flood tide again (Fig. 2d). Subsequently, 'Solomon' remained close inshore, though its movements remained linked to the phase of the tide.

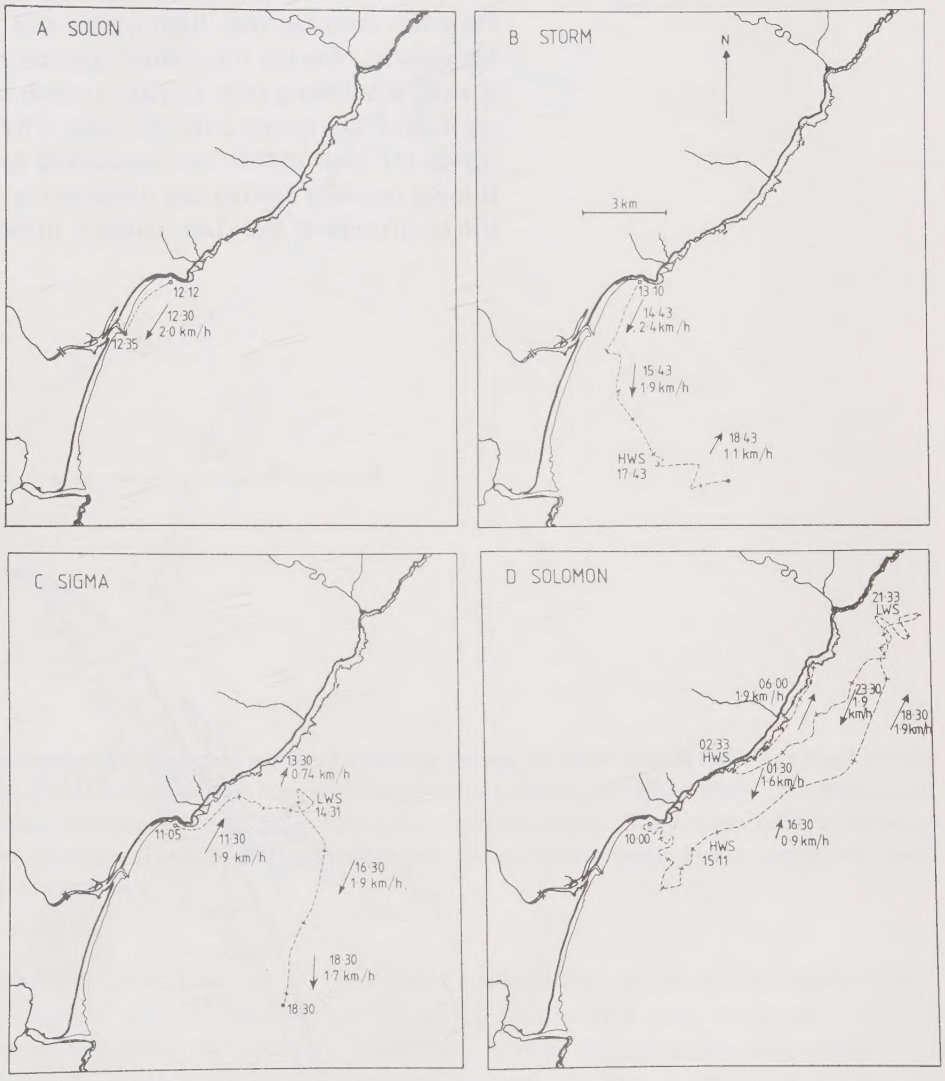

Figure 2. Movements of four Atlantic Salmon ('Solon', 'Storm', 'Sigma' and 'Solomon') off the Scottish east coast. The tracks of the fish are shown by dashed lines with hourly intervals marked with a slash. The arrows indicate the speed and direction of the predicted tidal stream. Open circle indicates start of track and closed circle the finish.

In general, the speed of the fish exceeded the predicted speed of flow of the tide by less than 1 km/h (ie a swimming speed relative to the water of less than half a body length per second). Exceptionally, 'Solomon' reached a swimming speed of 1.7 km/h (0.8 body lengths per second), while 'Solon' moving with the tide towards the river which it subsequently entered, swam at 5.2 km/h (2.4 body lengths per second).

These figures can only be approximate, since the speed of tidal flow could only be estimated, but they suggest that the fish were generally swimming well within their cruising capacity. Brett (1965) concluded that the most efficient swimming speed for the adult sockeye salmon was 1.1 mph (0.8 body lengths per second for a 60 cm fish).

Movements of fish close to the river

Three fish, 'Solon', 'Sabrina' and 'Sugar', entered the river North Esk. 'Solon' moved directly and quickly to the river mouth with the flood tide, entering the river 2½ hours before high water (Fig. 2a). On this day the river was in spate, following a period of heavy rain.

The other two fish entered the river mouth at times when the river was at more typical summer levels. Both fish reached the mouth at low slack water and passed to and fro across the river mouth, 'Sabrina' subsequently entering a few minutes after high water, and 'Sugar' entering about 3 hours after high water. During their initial approach to the river mouth both fish swam against the ebbing tide, though in each case this behaviour was preceded by periods of swimming with the tide. The to and fro movement by 'Sabrina' across the river mouth was associated with a change of tide, the fish continuing to swim against the direction of the tide until it reached a point on the north side of the river, when it turned and swam upstream (Fig. 3).

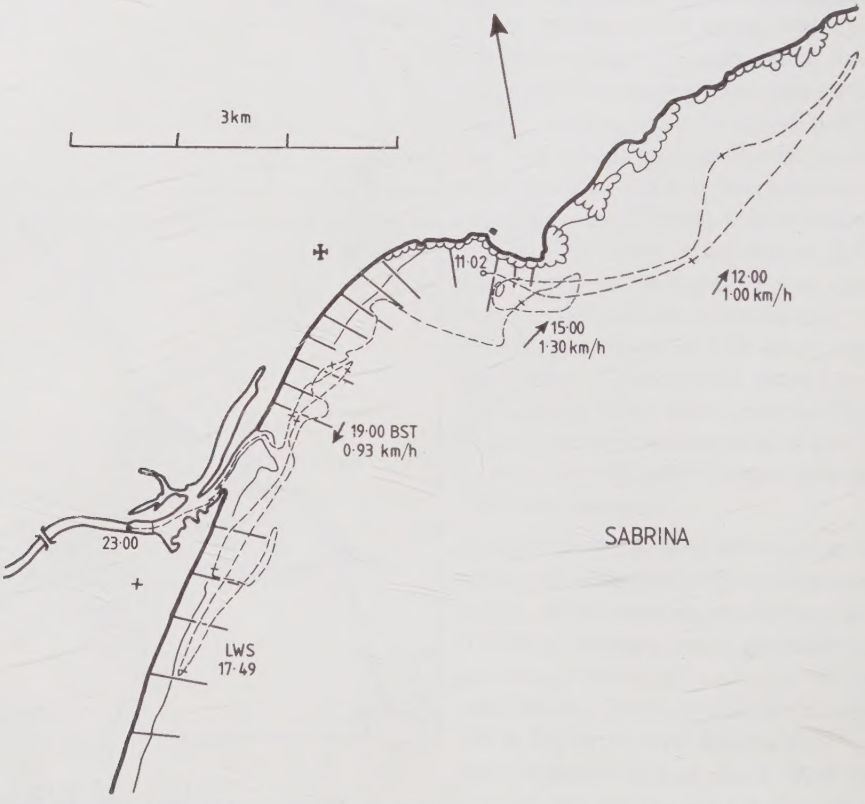

Figure 3. Movements of a grilse ('Sabrina') entering the River North Esk. The track of the fish is shown by a dashed line, with hourly intervals marked with a slash. The positions of salmon nets are shown as lines running out from the shore. The arrows indicate the speed and direction of the predicted tidal stream. Open circle indicates start of track and closed circle the finish.

'Sugar' also reversed direction to swim against the tidal flow after passing the river mouth. This behaviour resulted in the fish overshooting the river mouth on the north side followed by the fish reversing direction again, and then several more times before entering the river (Fig. 4). Both fish were often very close to the shore on their runs past the river mouth, often among breaking waves and in water of reduced salinity.

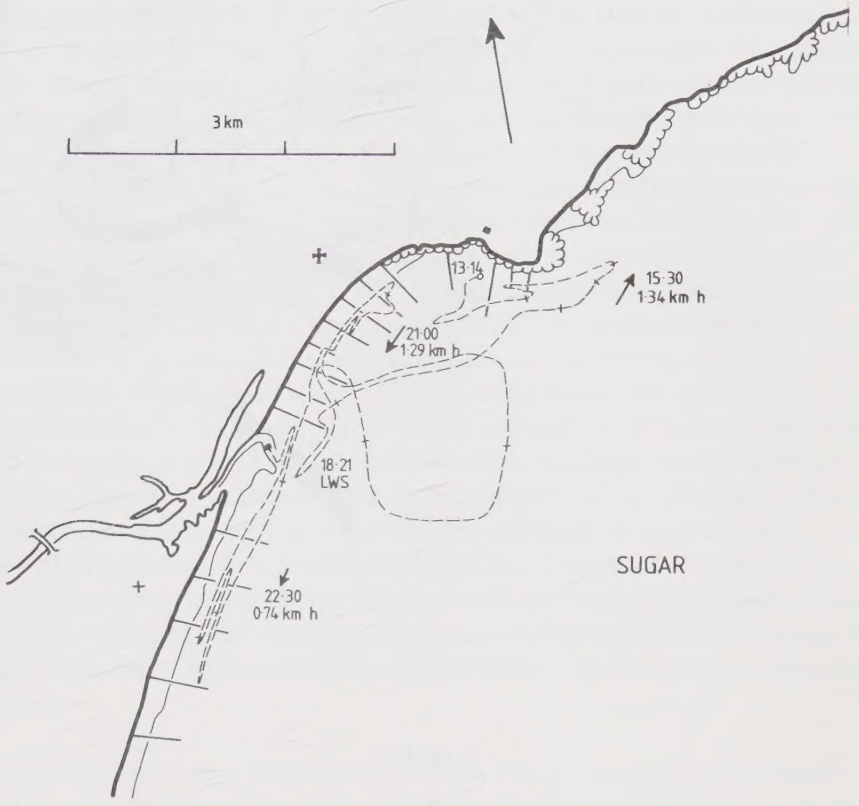

Figure 4. Movements of a grilse ('Sugar') entering the River North Esk. The track of the fish is shown by a dashed line, with hourly intervals marked with a slash. The position of salmon nets are shown as lines running out from the shore. The arrows indicate the speed and direction of the predicted tidal stream. Open circle indicates start of track and closed circle the finish.

Movements of fish in the river

Tracking carried out in the river itself showed that all three fish reached the first major pool in the river within 12 hours of entry, and remained stationery there for a period. 'Sabrina', in moving up to the pool, swam along the south bank of the river, falling back on two occasions but then resuming the upstream movement. A short period of 30 minutes was spent stationary in a backwater.

The avoidance of salmon nets

Four of the fish, 'Storm', 'Sigma', 'Sabrina' and 'Sugar' encountered salmon nets while moving along the coast, and each successfully negotiated the obstruction. 'Sabrina' and 'Sugar', in particular, repeatedly avoided capture by both bag and stake nets as they swam to and fro along the beaches to the north and south of the river North Esk.

The manner by which the fish avoided the net could not always be clearly determined, but in the majority of cases the fish seemed to swim between the leader and the cleek on one side, around the end of the leader and then out between the leader and the cleek on the opposite side (Fig. 5).

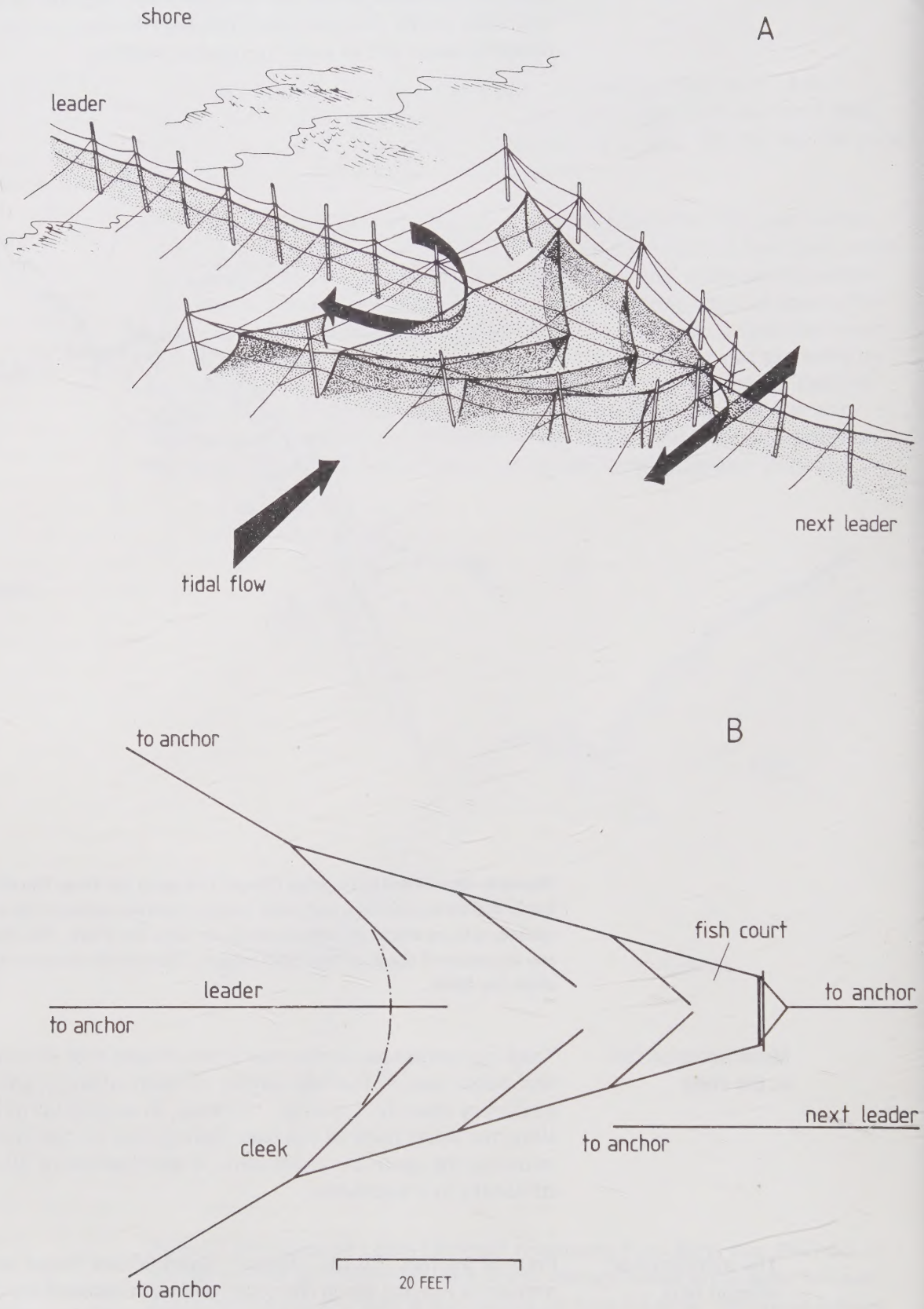

Figure 5. Avoidance of salmon nets by salmon.
a. Salmon stake net showing points where fish may pass through. Note that the net may be deformed by the tidal flow. The fish do not necessarily swim against the tide.
b. Plan view of a bag net. The position of the following leader is not always as shown, and the net itself may vary at different fishing stations.

In some cases, when negotiating a line of nets, the fish passing around the seaward end of the bag swam between the bag and the leader of the next net (Fig. 5). It also appeared that some fish swam beneath the leader.

Discussion

Almost no information is available on the behaviour of salmon returning from their feeding grounds. Too few fish have been captured at intermediate locations to allow speculation about the oceanic routes followed by the migrating fish, if indeed they do follow well defined routes from distinct feeding grounds. Royce, Smith & Hartt (1968) and Stasko, Sutterlin, Rommel & Elson (1973a) have concluded that the movements of the returning fish cannot be explained in terms of passive drift with water currents, since the residual velocities of oceanic currents are insufficient to account for some of the observed speeds of migration. In the absence of such a passive mechanism Stasko *et al.,* (1973a) conclude that the movements of Atlantic salmon are directed — that they are orientated to particular stimuli. A great variety of environmental factors have been proposed by different authors as providers of the necessary directional cues. An extreme view (Baker, 1978) proposed that the adult salmon is returning through an area familiar to it through previous exploration — a technique referred to by Harden Jones (1968) as pilotage. The opposing view, that fish reach their destinations largely by random wandering and passive drift, originally proposed by Huntsman (1934), has received some support from a numerical probability model developed by Saila & Shappy (1963). They proposed that salmon migrated by means of random searching combined with a low degree of orientation to some outside stimulus. Empirical values for the model parameters, taken from published data on the Pacific salmon, demonstrated the feasibility of the model and enabled the authors to conclude that it was unnecessary to invoke a precise orientation of the fish to explain the migration.

Evidence from our own experiments, where the movements of returning fish along the sea coast have been observed directly, is that salmon do not migrate by passive drift with tidal currents. Though the fish moved with the tide along the tidal axis their speed over the ground often appeared to exceed the current speed. Direct measurements of current speed were not made during the experiments and this conclusion can only be tentative. However, winds in the area at the time of study were slight and offshore, and were unlikely to influence the north-south currents away from predicted speeds and directions. We have no direct information on the sensory mechanisms by which orientation and movement with respect to the current might be maintained.

A simple back and forth movement with the tide, even amplified by the fish swimming with the tide, would not appear to be adequate by itself to bring the fish close to its natal river. There is a residual movement of the tide towards the south from Montrose Bay, but conventional tagging evidence from fish in this area strongly suggests that those fish which do not enter rivers in the bay move northwards (Pyefinch & Woodward, 1955; Shearer, 1958). Indeed, the large distances travelled relatively quickly by some tagged fish suggest that movement along the Scottish east coast can sometimes be quite strongly directional. Thus fish tagged near Montrose have travelled northwards at minimum overall speeds of up to 1.0 km/h (Pyefinch & Woodward, 1955) and others tagged at Altens, near Aberdeen, have been recovered at sites which require the fish to have travelled at an overall speed in excess of 0.6 km/h (Pyefinch & Shearer, 1957).

An economical mechanism by which a directional movement may take place is provided if the behaviour of the fish is different at different phases of the tide - as has been suggested for plaice, where the behaviour has been

termed selective tidal stream transport (Greer Walker, Harden Jones & Arnold, 1978). Thus, by varying depth (and hence varying the degree of passive carriage by stratified tidal currents), or by varying the speed and direction of motion relative to the tidal stream at different phases of the tide, the fish may move in a particular tidal direction with a minimum of effort. Such a mechanism has been clearly demonstrated for plaice in the southern North Sea (Greer Walker *et al.,* 1978), and its energetic efficiency has been commented upon by Weihs (1978).

The recovery of grilse and salmon tagged as smolts is less than 5%, even if fish caught at coastal netting stations are included (Table II). Unpublished data from smolt tagging in the North Esk by one of us (WMS) suggests that the majority of fish that return to freshwater reach their natal river, however; less than 1% stray to adjacent rivers and some of these captured fish might have returned to their natal river if left to find their way. Elson (1969) reports that less than 2% of Canadian recaptures are recorded from rivers other than the river of smolt origin. Other evidence for homing is given by Stasko *et al.,* (1973a). On the other hand, if recaptures at coastal netting stations are considered, there is a wide scatter of returning fish along the coast. In addition, returning fish which are tagged and released at coastal netting stations show a wide scatter (Pyefinch and Woodward, 1955; Pyefinch and Shearer, 1957; Shearer, 1958). Thus, salmon may make landfall well away from their natal rivers. It has been suggested that along the east coast of Scotland the fish reach land at particular points, one of these being Montrose Bay (Menzies, 1938) but the evidence for this is poor. It seems likely that there are two phases in the homing of salmon. In the first, the fish returns to the coastline. In the second, the fish move along the coast, making their entry to the natal river on the basis of local cues.

Table II

The recapture of tagged smolts as returning adults

River (and dates) of Tagging	Number of smolts tagged	Number of returning fish recaptured in				Total number of smolts recaptured (including fish caught in the open sea and at coastal netting stations)		Authority
		a) Home river		b) above tidal reaches of other rivers				
North Esk (1961 - 1976)	117,900	877	(0.7)	32	(0.02)	4,616	(3.9)	Shearer (unpublished data)
Tay (1967 - 1973)	34,500	738	(2.1)	2	(0.006)	1,047	(3.0)	Struthers (1975)
Dee (Aberdeenshire) (1967 - 1973)	15,500	*118	(0.8)	+36	(0.23)	458	(3.0)	Hay (personal) communication)
Coquet (1952 - 1957)	23,400	41	(0.2)	3	(0.01)	478	(2.0)	Swain (personal communication)
Usk (1959 - 1964)	10,400	20	(0.2)	2	(0.02)	53	(0.5)	"
Wye (1959 - 1964)	21,300	39	(0.2)	3	(0.01)	82	(0.4)	"
Severn (1959 - 1964)	23,200	39	(0.2)	4	(0.02)	93	(0.4)	"
Axe (1960 - 1973)	47,700	*740	(1.6)	6	(0.01)	928	(1.9)	"
Ure (1968 - 1978)	16,200	3	(0.02)	6	(0.04)	174	(1.1)	"

Figures in brackets are percentages of smolts tagged

*Total includes fish caught in experiment trap

+21(58%) caught in North Esk

Three of our acoustically tagged fish entered the river North Esk. One fish approached the river mouth moving with the flood tide when the river was in spate, entering the river directly at high water. In stemming the fast flowing river the behaviour of the fish at some point changed from swimming with the tidal current to swimming against the flow of the river. The other

two fish entered the river more gradually, spending some time in the sea off the river mouth. The behaviour of these fish differed from that of the fish tracked further offshore, in that they showed prolonged periods of swimming against the tidal flow before entering the river. We can only speculate on the factors resulting in this change of behaviour. The current issuing from a river is thought to be an important guide to the fish migrating into it (Huntsman, 1934), and entry is often associated with the occurrence of freshets (Huntsman, 1948; Alabaster, 1970 and others). Deelder (1958) has shown that the responses of elvers to currents changes in the presence of fresh water, and it is possible that similar changes may occur in the salmon. Perhaps in the presence of low salinity water or more specific chemical cues from the North Esk the fish reverse their rheotactic responses, and stem the current. Thus, chemical cues may initiate the change in behaviour, the actual orientation of the fish being mediated by a response to water current.

The importance of olfactory cues to migrating salmon in the Baltic has been clearly demonstrated by Bertmar & Toft (1969). Anosmic fish did not home, while control fish did. That returning salmon stem currents close to the coast and in estuaries has also been clearly established by other workers (Hasler, Horrall, Stasko & Dizon, 1970; Stasko, Horrall, Hasler & Stasko, 1973b). The swimming of salmon close to the surface, reported by Holand & Mohus (1976) and Stasko *et al.* (1973b) would facilitate contact of the fish with low density water from the river mouth. Many laboratory studies have demonstrated the extreme acuity of the fish olfactory system, and have confirmed that fish can distinguish between the odours of natural waters (for a recent study see Bodznick, 1978). Solomon (1973) presents evidence that the homing of adult Atlantic salmon may be largely dependent upon pheromones released by other individuals in the river. Bodznick (1978), on the other hand, working with sockeye salmon in fresh water, has suggested that the calcium level of natural waters is important in guiding the fish to its home tributary.

The small river North Esk is very suitable for examining the entry of salmon to fresh water. The estuary is short and narrow, and the fish may reach full fresh water with little swimming effort. Our study showed that one fish ('Solon') made the transition from full sea water (salinity 34%) to full fresh water in less than 30 hours, suggesting that the osmotic problems associated with the change are not a severe deterrent to fish entering the river. This is borne out by the ease with which fish caught in bag-nets can adapt to fresh water; the fish can survive direct transfer to fresh water.

A clear point established by our tracking study is that individual salmon often avoid capture by bag and stake nets placed along the coast. Though a proportion of fish tagged at some coastal netting stations are recaptured at other stations, our observations suggest that this capture rate reflects the frequency with which salmon encounter these nets, rather than the efficiency of the nets *per se.* The presence of the nets certainly does not seem to significantly impede the entry of fish into the river. Though we found that changes in the direction of movement of the fish were often associated with the fish encountering a net, the fish often succeeded in negotiating the obstacle, either eventually passing through the obstruction, or swimming around the end of it.

Acknowledgements

Our tracking studies could not have been performed without the willing help of our colleagues A. Dunthorn, C. Hall, K. Horner, A.D.F. Johnstone and C. Robb. We thank them, and Messrs Jos. Johnston and Sons Ltd and their Skipper T. Dalgarno and crew at Rockhall.

Summary Atlantic salmon caught in the sea at a netting station on the east coast of Scotland were tagged with acoustic transmitters, released and followed from a small boat. The movements of six grilse were studied, three of these eventually entering the river North Esk. In the sea the fish moved with the tide. On reaching the river mouth, however, the behaviour of the fish reversed, as they stemmed the fresh water current.

During the tracking it was clearly established that salmon can avoid capture by many of the bag and stake nets they encounter along the coast, passing through or around these fishing gears.

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